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Communication: Animal Steps on the Road to Syntax?

Andrew F. Russell¹ and Simon W. Townsend^{2,3}

¹Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Cornwall TR10 9FE, UK

²Department of Psychology, University of Warwick, University Road, Coventry CV4 7AL, UK

³Department of Comparative Linguistics, University of Zurich, Plattenstrasse 54, 8032 Zurich, Switzerland

Correspondence: a.russell@exeter.ac.uk (A.F.R.), simonwilliam.townsend@uzh.ch (S.W.T.)

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From tool use to teaching, proto-forms of ‘human traits’ are being discovered in animals. But what of language? New evidence suggests that a garden bird has hopped on the long road to syntax, an integral component of language.

Of all the traits considered to be uniquely human, language is amongst the most defining. No other extant animal species naturally uses language, and language has likely been pivotal to humanity's current success [1]. Understanding the emergence of humanity thus, in part, requires an understanding of the emergence of language. A prevailing hypothesis is that the core components of language evolved uniquely during hominin evolution [2]. But as reported by Suzuki *et al.* [3] in this issue of *Current Biology*, new work on the Japanese tit (*Parus minor*), a common garden bird of eastern Asia, provides compelling evidence that animals can compose meaningful sequences by joining specific calls in rule-guided combinations — a requisite of compositional syntax [4].

Human language is characterised by the ability to combine sounds generatively [4]. First, a finite number of meaningless sounds (phonemes) are arranged to make an extensive array of morphemes and words (phonology). Second, morphemes and words are then further organised into myriad compound words, phrases and sentences, which is referred to here as

compositional syntax [4,5]. A notable feature of the latter process is that words maintain their identity across compositions, allowing the meaning of the whole to be derived from its parts, and that rules — sometimes referred to as syntactic operations — underpin the association between word composition and information transfer. For example, the word *ship* maintains its basic meaning, and so adds to the meaning of the whole, when preceded by *cargo* or *cruise*, but the

constructions lose intended meaning when order is reversed.

Experimental evidence from a handful of social monkey and bird species suggests that the ability to produce compositional sequences is not uniquely human (Figure 1). For example, male Campbell's monkeys (*Cercopithecus campbelli*) of west Africa use two distinct calls to signal terrestrial versus aerial threats. When the exact threat is ambiguous, however, either alarm can



Figure 1. Disparate taxa show proto compositional syntax.

Playback experiments confirm the essence of compositional syntax is used by primates and unrelated birds in their communication systems: left, Campbell's monkey (credit Erin Kane); middle, southern pied babbler (credit Dave Humphries); and right, Japanese tit (credit Toshitaka Suzuki).

Table 1. Compositional syntax: rules and processing

Test call composition	Response	Take-home point
Alert (JT) + Recruitment (JT)	<i>Approach speaker <2m and scanning – mirroring normal mobbing response to natural compositions</i>	Response consistent with CS: 2 independent calls are used in stereotypic combination to generate new information that is related to the meaning of the constituent parts
Alert (JT) + Recruitment (WT)	Response equivalent to natural playbacks above	Suggests composition not processed as stand-alone unit, and meaning is encoded in the constituent parts
Recruitment (WT) + Alert (JT)	No consistent response	Order matters: rules underpin meaning in novel sequences
Alert (JT) + Alert (WT) or Alert (WT) + Alert (JT)	No consistent response	Composition matters: compositions beginning with alert calls are not sufficient to generate natural response

New evidence using responses to novel playback sequences (normal font) further links compositional syntax in animals and humans, by demonstrating that ordering rules underpin information transfer and compositions are not processed as stand-alone calls [3]. JT and WT signify when calls played back derive from Japanese tits versus willow tits, respectively; CS refers to compositional syntax. Text in italics depicts baseline response to natural alert-recruitment sequences [10].

be generalised or weakened through the addition of another vocal unit onto the end of the alarm [6,7]. One interpretation compares this example to the addition of the meaning-bearing syntactic unit *like* in English, which serves to change the meaning of a word, from specific, for example *eagle*, to more general, for example *eagle-like*. Hence this can be considered as a rudimentary compositional system ([5], see also [8]).

Two social birds have also been shown to combine independently occurring calls in compositional-like ways. The southern pied babbler (*Turdoides bicolor*), a social bird from semi-arid southern Africa, uses one call to signal low-urgency threats and another to recruit group members to a foraging patch or roost site [9]. When used in combination, however, individuals recruit to mob a predator: playbacks of natural and manipulated call stimuli confirm that it is the combination of the two calls that generates the new response. Interestingly, experiments with Japanese tits confirm that alert and recruitment calls are also combined to similar ends in another bird species [10]. Together, these studies suggest multiple independent evolutionary origins of the ability to compose calls into higher-order, meaningful syntactic structures.

Demonstrating the degrees to which these data resemble compositional syntax in human language requires testing whether basic rules underpin the association between call compositions and information transfer; and whether the meaning encoded in compositions is

really the product of the information encoded in the component parts (i.e. that compositions are not processed as stand-alone, holistic calls). Testing each of these points is not straightforward. First, whilst the conserved structure of compositions suggests that ordering rules might underpin information transfer, testing order effects is difficult because receivers might respond more strongly to naturally occurring playback sequences, not because order helps to resolve meaning, but simply because natural orders are more familiar. Second, confirming that the meaning of the whole is related to the parts is inherently complicated by the fact that compositions might be processed as stand-alone units, rather than products of comprising calls [8]. One means of testing each point in humans is to investigate how subjects process novel combinations which are unfamiliar and cannot have been prior-learned [8,11]. The challenge of implementing this approach in animals lies with obtaining novel, yet behaviourally-relevant, call compositions.

Heterospecific Calls as the Building Blocks for Novel Combinations?

In their new paper, Suzuki *et al.* [3] cleverly generated novel playback compositions for Japanese tits by incorporating equivalent calls of willow tits (*Poecile montanus*), a flock-mate of Japanese tits (Table 1). For example, by exchanging the recruitment calls of Japanese tits with that of recruitment calls from willow tits in alert-recruitment call sequences, the authors were able to test the role of call

order and composition in novel playback sequences. The key predictions tested were: first, if information is generated by call-order, maintenance *versus* manipulation of order in novel sequences should lead to appropriate *versus* inappropriate responses, respectively; and second, if the meaning encoded in each of the two constituent calls dictates the response to the composition, then they should be able to respond accordingly to novel compounds that encode equivalent information (see Table 1 for full details).

Suzuki *et al.* [3] found that novel combinations comprising alert calls (from Japanese tit) and recruitment calls (from willow tits) led to equivalent responses as natural alert-recruitment playback sequences from Japanese tits, but that this was not the case when the order was reversed. Thus, **order-rules do underpin information transfer**. Further, by testing responses to artificial compositional sequences of Japanese-alert and willow-alert, and *vice versa*, the authors demonstrated that beginning call sequences with alert calls was insufficient to generate the normal response: in neither case did the receivers approach the speaker in a way reminiscent of responses to alert-recruitment sequences. Finally, the authors also confirmed that the responses were not confounded by any similarity between the recruitment calls of Japanese and willow tits. Together, these results not only show that, in Japanese tits, order-rules underpin information transfer in call compositions, but strongly suggest that

they extract the overall meaning of the composition from the meaning encoded in each component part [3].

Implications for Proto-forms of Syntactic Communication and Future Directions

These new data, in conjunction with those of others, have two key implications. First, they help bridge the assumed chasm separating human and animal communication, and lend support to the growing consensus that animals can combine vocalisations to expand their repertoires [9,12–14]. Second, they hint at a converging pattern in the emergence of syntax-like communication in animals, with at least some parallels with human syntax. Indeed, it is noteworthy that there appears to be concordance between syntax-like communication in animals and the way in which syntax initially develops in children where single words are combined into larger two-word constructions [4,11]. It is therefore not implausible that a key first step along the long path culminating in a fully-fledged productive syntactic system is a two-unit composition [9,15].

The emerging picture is that animals are capable of combining vocalisations into larger meaningful structures, with potential parallels to combinatorial structures in human language [4,5]. We suggest two avenues for future research in animal compositional syntax. First, documenting compositionality in more systems is required to establish how widespread this communicative capacity is, its general form and function, and the selection pressures underpinning its emergence. Second, although compositional, the structures so far identified in animals pale in comparison to the productive, hierarchical structures that characterise human linguistic systems [16]. Further studies are required to determine whether animals can communicate using compositions of more than two calls, and whether they can use the same calls flexibly in different configurations to further increase their repertoire. Testing the degrees to which these and other components of compositional systems concord with human compositional syntax will elucidate how far animals have travelled on the road to syntax, and offer insights into early forms of syntax in our ancestors.

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Spatial Cognition: Grid Cells Harbour Three Complementary Positional Codes

Martin Stemmler^{1,2} and Andreas V.M. Herz^{1,2,*}

¹Faculty of Biology, Ludwig-Maximilians-Universität München, 82152 Martinsried, Germany

²Bernstein Center for Computational Neuroscience Munich, 82152 Martinsried, Germany

*Correspondence: herz@bio.lmu.de

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The firing fields of mammalian grid cells, which map an animal's environment, lie on hexagonal lattices. Three new studies report significant field-to-field differences in the firing rates, a finding with far-reaching consequences for how grid fields form and encode spatial information.

Grid cells in the medial entorhinal cortex (MEC) represent space using hexagonal lattices [1], complementing the localized spatial representation of hippocampal place cells [2]. Environmental boundaries both calibrate and deform grid-cell

lattices [3,4]. These distortions and dislocations have sparked debate as to whether the hexagonal grid is the brain's metric for space [3]. Three recent papers [5–7] — one in this issue of *Current Biology* [7] — add a new twist to the